

PROCEEDINGS
OF
THE ROYAL SOCIETY.

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March 24, 1881.

THE PRESIDENT in the Chair.

The Presents received were laid on the table, and thanks ordered for them.

The following Papers were read:—

- I. THE CROONIAN LECTURE.—“Observations on the Locomotor System of Echinodermata.” By GEORGE J. ROMANES, M.A., F.R.S., and Professor JAMES C. EWART, M.D. Received March 5, 1881.

(Abstract.)

I.—MORPHOLOGY.

In *Holothuria* the polian vesicle opens freely into a wide circular canal a short distance from the termination of the stone canal. From this circular canal five lozenge-shaped sinuses project forwards, and from each of these two large oval sinuses run forward parallel with each other—the ten oval sinuses becoming continuous with the hollow stems of the tentacles. Injection of the polian vesicle shows that it forms one continuous tube system with the circular canal and its sinuses, oval sinuses and tentacles, ampullæ and pedicels. Unless the pressure is kept up for a considerable time there is no penetration of the injected fluid into the stone canal, and either the ring, the vesicle, or a sinus gives way before the fluid reaches the madreporic plate. Specimens injected with a gelatine mass show that each canal sinus opens into a cæcal tube, which runs forwards internal to the sinuses of the tentacles as far as a wide circum-oral space. This space com-

municates by well-defined apertures with that portion of the body cavity which lies between the sinuses and the œsophagus, and which is reached through the circular apertures between the sinuses of the circular canal. Each canal sinus has three other apertures in its walls. It opens by a small round aperture into a radial canal, and the two other apertures occur as minute slits, one at each side of the orifice of the radial canal leading into the adjacent tentacle sinuses. When the tentacle into which the sinus opens is protruded, there is no constriction between the sinus and the tentacle; but when the tentacle is retracted, there is a well-marked constriction at the junction of the sinus with the tentacle. The eversion of the perisome and the protrusion of the tentacles are effected chiefly by the shortening of the polian vesicle and the constriction of the longitudinal muscular bands, which run from the inner surface of the body wall between each two adjacent tentacle-sinuses; but the circular fibres of the body wall also assist in the process by contracting immediately behind the group of sinuses, so as to act on them by direct pressure, and also indirectly by forcing the body fluid against them.

The amount of the body cavity fluid is constantly changing. At the entrance to the cloacal chamber there is a circular valve which is constantly dilating and contracting, except when the aboral end of the animal is forcibly retracted. When open, this valve allows water to pass into the respiratory tree; when it begins to retract, water escapes from the cloaca. This alternate opening and closing takes place with perfect rhythm, at a rate of about six revolutions per minute. At the end of every seventh or eighth revolution a large stream of clear water is ejected, which sometimes contains sand and the remains of food particles. When the tentacles are being protruded, more water is taken in at the cloaca than escapes; on the other hand, retraction of the tentacles is preceded by an escape of a large stream of water.

In *Echinus*, two tubes spring from the under surface of the madreporic plate. The one is dilated at its origin, so as to include the greater portion of the plate, and ends in the so-called heart; the other is small, deeply pigmented, and runs along a groove in the heart to open into a circular canal at the base of the lantern. From the under aspect of this circular canal the five radial ambulacral vessels take their origin. Immediately within the oral margin of the shell, and alternating with the inner row of pedicels, are the five pairs of "tree-like organs." If a fine glass cannula be forced through the membrane which extends from the apex of each tooth to the oral margin of the interambulacral plates and sides of the alveoli, coloured fluids may be injected into the space between the membrane and the alveoli of the lantern; the fluid then slowly diffuses upwards into the vesicles around the apices of the teeth. It reaches these

vesicles partly by passing directly upwards external to the alveoli, and partly by passing into the cavities of the alveoli and ascending through the circular sinus.

In *Spatangus* the ambulacral circumoral canal has no polian vesicles or sinuses developed in connexion with it. Some of the pedicels have suckers, others are conical and devoid of them, while others again are flattened at their tips, and sometimes split up into segments.

If one of the arms of *Solaster papposa* is divided transversely, and a coloured fluid introduced into the open end of the radial canal, the ampullæ and pedicels of the injected arm are at once distended. The fluid next penetrates the circular canal, polian vesicles, ampullæ, and pedicels of the other arms; but unless considerable pressure be kept up for some time, none of the solution enters the madreporic canal. If, however, the pressure is maintained for several hours with a column of fluid 2 feet high, the fluid ascends through the stone canal and diffuses slowly through the madreporic plate. When a thin slice is then shaved off the plate, the fluid is observed escaping from a small circumscribed area situated between the centre and the margin of the plate, and corresponding in size and position with the termination of the stone canal on the inner surface. The stone canal, gradually increasing in diameter as it passes inwards from the madreporic plate, runs obliquely over its accompanying sinus, till it finally hooks round this sinus to open into the circular canal. Springing from this canal and opposite to each inter-radial space (with the exception of the space occupied by the stone canal) is a polian vesicle. The size and form of these vesicles are largely determined by the amount of fluid in the pedicels. In none of the injected specimens was there any evidence of a communication between the ambulacral vessels and the body cavity, or between the ambulacral and the blood (neural) vessels. There was, however, abundant evidence of communication between the latter and the exterior. When a cannula was introduced into the outer end of the sinus, a coloured solution could be easily forced through the sinus into the circular blood-vessel, and from this into the radial blood-vessels. But when the cannula was introduced into the proximal end of the sinus, the solution rapidly rushed along the sinus and escaped through the madreporic plate, proving that the blood-vessels of *Solaster* communicate far more freely with the exterior than do the water-vessels.

The ambulacral system of the common star-fish only differs from that of the sun-star in having no polian vesicles. *Astropecten*, on the other hand, has polian vesicles; but in it the pedicels have departed from the usual form in being short, conical, and unprovided with terminal suckers. In *Ophiura* the pedicels are morphologically similar to those of *Astropecten*, though shorter and more slender.

They diminish in size as they proceed outwards, and at the ends of the arms are scarcely visible.

*Nervous System of Echinus.*

The internal nervous system of *Echinus* consists of five radial trunks, which may be traced from the ocular plates along the ambulacral areas external to the radial canals to the oral floor, where they bifurcate and unite with each other so as to form the pentagonal nerve-ring. This ring lies between the œsophagus and the tips of the teeth which project from the lantern. Small branches leave the ring and supply the œsophagus, and lateral branches arise from the several trunks to escape with the pedicels through the apertures of the pore plates. Each trunk lies in a sinus situated between the lining membrane of the shell and the ambulacral radial canal. The lateral branches which accompany the first series of pedicels through the oral floor are large and deeply pigmented. The branches within the auricles are small; those external to the auricles gradually increase in size until the equator is reached, and from the equator to the ocular plates they diminish in size. At the equator, the trunk is wider than at either pole, and it is often partially divided for some distance at each side of the equator by a deep longitudinal fissure.

When the nerve-trunk, after being stained with chloride of gold or with osmic acid, is removed from its sinus, it is seen to be enveloped by a thin fibrous sheath. This sheath contains numerous large pigment cells, and has scattered over it irregular masses of protoplasm which have been deposited from the fluid of the neural sinus.

When the sheath is removed, the trunk is seen to consist of delicate fibres and of fusiform cells. The cells consist of a nucleus and a thin layer of protoplasm, which projects at each end, and terminates in a nerve-fibre.

The lateral branches of the trunk escape along with and are partly distributed to the pedicels; the remainder break up into delicate filaments which radiate from the base of the pedicel under the surface epithelium. When one of the large branches already referred to as escaping with the inner row of pedicels is traced through the oral floor, after sending a branch to the foot, it breaks up into delicate fibres, some of which run towards the bases of the adjacent spines and pedicellariæ, while others run inwards a short distance towards the oral aperture.

Either in connexion with, or anatomically independent of, these filaments from the lateral branches of the nerve-trunks, there arises an external plexus lying almost immediately under the surface epithelium and extending from the shell to the spines and pedicellariæ. The fibres of this plexus closely resemble the fibres of the lateral branches of the trunk, but generally they are smaller in size and have

a distinct connexion with nerve-cells. The cells consist of an oval nucleus and of a layer of protoplasm, which is generally seen to project in two, or sometimes in three, directions—the several processes often uniting with similar processes from adjacent cells, so as to form a fibro-cellular chain or network.

In preparations from portions of *Echini* treated with both chloride of gold and osmic acid, we have succeeded in tracing the plexus over the surface of the shell between the spines and pedicellariæ, and from the surface of the shell to the capsular muscles at the bases of the spines; we repeatedly observed delicate fibres passing beyond the muscles to end apparently under the epithelium over the surface of the spines.

In the case of the pedicellariæ the plexus on reaching the stem runs along between the calcareous stem and the surface epithelium, to reach and extend over and between the muscular and connective tissue fibres between the stem and the bases of the mandibles. The plexus, now in the form of exceedingly delicate fibres connecting small bipolar cells, reaches the special muscles of the mandibles. In several preparations delicate fibres appeared to extend towards the sensitive epithelial pad situated on the inner surface of each mandible a short distance from the apex. Although this plexus is especially related to the muscular fibres, lying over and dipping in between them, it is also related to the surface epithelium, and delicate fibres often extend from it to end under or between the epithelial cells.

## II.—PHYSIOLOGY.

1. *Natural Movements.*—The ordinary crawling movements of *Astropecten aurantiacus* are peculiar, the ambulacral feet acting the part of walking-poles and cilia combined. Brittle-stars progress by using two opposite arms upon the floor of the tank, with a movement like swimming; at each stroke the animal advances with a sort of leap, and can thus travel at the rate of six feet per minute. The ordinary progression of *Echinus* and *Spatangus* is assisted by the co-ordinated action of the spines, and when placed upon a flat surface out of the water the animal advances by means of its spines alone. In *Echinus* the lantern and pedicellariæ are also used to assist in locomotion.

All the Echinodermata that we have observed are able, when placed upon their dorsal surfaces on the floor of a tank, to recover their normal position on their oral surface. The common star-fish does so by twisting the ends of two or more of its rays round, so as to bring its terminal suckers into action upon the floor of the tank, and then, by a successive and similar action of the suckers further back in the series, the whole ray is progressively twisted round, so that its ambulacral surface is applied flat against the floor. The rays which perform

this action twist their semi-spirals in the same direction, and by their concerted action serve to drag the disk and the remaining rays over themselves as a fulcrum. Other species of star-fish, which have not their ambulacral suckers sufficiently developed to act in this way, execute their righting movements by doubling under two or three of their adjacent rays, and turning a somersault over them, as in the previous case. *Echinus* rights itself when placed on its aboral pole, by the successive action of two or three adjacent rows of suckers, so gradually rising from aboral pole to equator, and then as gradually falling from equator to oral pole. *Spatangus* executes a similar manoeuvre entirely by the successive pushing and propping action of its longer spines.

2. *Stimulation*.—All the echinoderms that we have observed seek to escape from injury in a direct line from the source of stimulation. If two points of the surface are stimulated, the direction of escape is the diagonal between them. When several points all round the animal are simultaneously stimulated, the direction of advance becomes uncertain, with a marked tendency to rotation upon the vertical axis. If a short interval of time be allowed to elapse between the application of two successive stimuli, the direction of advance will be in a straight line from the stimulus applied latest. If a circular band of injury be quickly made all the way round the equator of *Echinus*, the animal crawls away from the broadest part of the band—*i.e.*, from the greatest amount of injury.

The external nerve plexus supplies innervation to three sets of organs—the pedicels, the spines, and the pedicellariæ; for when any part of the external surface of *Echinus* is touched, all the pedicels, spines, and pedicellariæ within reach of the point that is touched immediately approximate and close in upon the point, so holding fast to whatever body may be used as the instrument of stimulation. In executing this combined movement the pedicellariæ are the most active, the spines somewhat slower, and the pedicels very much slower. If the shape of the stimulating body admits of it, the forceps of the pedicellariæ seize the body and hold it till the spines and pedicels come up to assist.

And here we have proof of the function of the pedicellariæ. In climbing perpendicular or inclined surfaces of rock covered with waving sea-weeds, it must be no small advantage to an echinus to be provided on all sides with a multitude of forceps adapted, as described, to the instantaneous grasping and arresting of a passing frond; for, in this way, not only is an immediate hold obtained, but a moving piece of seaweed is held steady till the pedicels have time to establish a further and more permanent hold upon it with their sucking disks. That this is the chief function of the pedicellariæ is indicated by the facts that, 1st, if a piece of seaweed is drawn over the surface of an *Echinus*, this function may clearly be seen to be performed; 2nd, the wonder-

fully tenacious grasp of the forceps is timed as to its duration with an apparent reference to the requirements of the pedicels, for after lasting about two minutes (which is about the time required for the suckers to bend over and fix themselves to the object held by the pedicellariæ, if such should be a suitable one), this wonderfully tenacious grasp is spontaneously released; and, 3rd, the most excitable part of the trident pedicellariæ is the inner surface of the mandibles, about a third of the way down their serrated edges—*i.e.*, the part which a moving body cannot touch without being well within the grasp of the forceps. When the forceps are closed, they may generally be made immediately to expand by gently stroking the external surface of their bases.

With regard to stimulation of the spines, if severe irritation be applied to any part of the external or internal surface of an *Echinus*, the spines all over the animal take on an active bristling movement. The tubercles at the bases of the spines are the most irritable points on the external surface.

With regard to stimulation of the pedicels, if an irritant be applied to any part of a row, all the pedicels in that row retract in succession from the seat of stimulation, but the influence does not extend to other rows. A contrary effect is produced by applying an irritant to any part of the external nerve plexus, all the pedicels being then stimulated into increased activity. Of these antagonistic influences, the former, or inhibitory one, is the stronger, for if they are both in operation at the same time the pedicels are retracted.

Star-fish (with the exception of brittle-stars) and *Echini* crawl towards, and remain in, the light; but when their eye-spots are removed they no longer do so. When their eye-spots are left intact they can distinguish light of very feeble intensity.

3. *Section.*—Single rays detached from the organism crawl as fast and in as determinate a direction as do entire animals. They also crawl towards light, away from injuries, up perpendicular surfaces, and, when inverted, right themselves. Dividing the ray-nerve in any part of its length has the effect of destroying all physiological continuity between the pedicels on either side of the division. Severing the nerve at the origin of each ray, or severing the nerve-ring between each ray, has the effect of totally destroying all co-ordination among the rays; therefore, the animal can no longer crawl away from injuries; and, when inverted, it forms no definite plan for righting itself. Each ray acting for itself, without reference to the others, there is, as a result, a promiscuous distribution of spirals and doublings, which, as often as not, are acting in antagonism to one another. This division of the nerves usually induces, for some time after the operation, more or less tetanic-like rigidity of the rays. The operation, however, although so completely destroying physio-

logical continuity in the rows of pedicels and the muscular system of the rays, does not destroy, or perceptibly impair, physiological continuity in the external nerve-plexus; for however much the nerve-ring and nerve-trunks may be injured, stimulation on the dorsal surface of the animal throws all the pedicels and the muscular system of the rays into active movement. This fact proves that the pedicels and the muscles are all held in nervous connexion with one another by the external plexus, without reference to the integrity of the main trunks.

If a cork-borer be rotated against the external surface of an *Echinus* till the calcareous substance of the shell is reached, and therefore a continuous circular section of the overlying tissues effected, the spines and pedicellariæ within the circular area are physiologically separated from those without it, as regards their local reflex irritability. That is to say, if any part of this circular area is stimulated, all the spines and pedicellariæ within that area immediately respond to the stimulation in the ordinary way, while none of the spines or pedicellariæ surrounding the area are affected, and conversely. Therefore we conclude that the function of the spines and pedicellariæ of localising and gathering round a seat of stimulation is exclusively dependent upon the external nervous plexus. If the line of injury is not a closed curve, so as not to produce a physiological island, the stimulating influence will radiate in straight lines from its source, but will not irradiate round the ends of the curve or line of injury.

Although the nervous connexions on which the spines and pedicellariæ depend for their function of localising and closing round a seat of stimulation are thus shown to be completely destroyed by injury of the external plexus, other nervous connexions, upon which another function of the spines depends, are not in the smallest degree impaired by such injury. This other function is that which brings about the general co-ordinated action of all the spines for the purposes of locomotion. That this function is not impaired by injury of the external plexus is proved by severely stimulating an area within a closed line of injury on the surface of the shell; all the spines over the whole surface of the animal then manifest their bristling movements, and by their co-ordinated action convey the animal in a straight line of escape from the source of irritation.

We have, therefore, to distinguish between what may be called the local reflex function of the spines, which they show in common with the pedicellariæ and which is exclusively dependent upon the external plexus, and what we may call the universal reflex function of the spines, which consists in their general co-ordinated action for the purposes of locomotion and which is wholly independent of the external plexus. Evidently, therefore, this more universal function must depend upon some other set of nervous connexions (which, however, we have not been able to detect histologically), and experi-

ment shows that these, if present, are distributed over all the *internal* surface of the shell. For if the internal surface be painted with acid, or scoured out with emery paper and brick-dust, the spines and pedicellariæ, after a short period of increased activity or bristling, become perfectly quiescent, lie flat, and lose both their spontaneity and irritability. After a few hours, however, the spontaneity and irritability of the spines return, though in a feeble degree, and also those of the pedicellariæ in a more marked degree. These effects take place over the whole external surface of the shell, if the whole of the internal surface be painted with acid or scoured with brick-dust; but if any part of the external surface be left unpainted or unscoured, the corresponding part of the external surface remains uninjured. From these experiments we conclude:—1st, that the general co-ordination of the spines is wholly dependent on the integrity of the hypothetical internal plexus; 2nd, that the hypothetical internal plexus is everywhere in intimate connexion with the external, apparently through the calcareous substance of the shell; and 3rd, that complete destruction of the former, while profoundly influencing through shock the functions of the latter, nevertheless does not wholly destroy them.

*Echini* may be divided into pieces, and the pedicels, spines, and pedicellariæ upon these pieces will continue to exhibit their functions of local reflex irritability, however small the pieces may be. If an entire double row of pedicels be divided out as a segment, and then placed upon its aboral end, it may rear itself up on its oral end by the successive action of its pedicels, and then proceed to crawl about the floor of the tank. We have therefore to meet the question: Is the action of the ambulacral feet in executing these righting movements of a merely serial kind—*a*, *b*, and *c*, first securing their hold on the tank floor, owing to the stimulus supplied by contact, and then by their traction tilting over the globe till *d*, *e*, and *f* are able to touch the floor, and so on; or does the righting action depend upon nervous co-ordination? We conclude that both principles are combined, the action of the pedicels being serial, but also assisted by nervous co-ordination. This conclusion is sustained by the experiment of shaving off the spines and pedicels over one-half of one hemisphere—*i.e.*, the half from the equator to the oral pole. When then inverted and forced to use their mutilated pedicel-rows, the *Echini* reared themselves upon their equators, and then, having no more pedicels wherewith to continue the manœuvre, came to rest. This rest was permanent, the animal remaining, if accidents were excluded, upon its equator till it died. The question, then, here seems to resolve itself simply into this: Is the mechanism of the pedicels so constructed as to ensure that their serial action shall always take place in the same direction? For if it can be shown that their serial action may take place indifferently in

either direction, it would follow that the persistency with which the partly shaved *Echini* continue reared upon their equators, is the expression of some stimulus (such as a sense of gravity) continuously acting upon some central apparatus, and impelling the latter to a continuous, though fruitless, endeavour to co-ordinate the absent pedicels. If the pedicels are able to act serially in either direction, there is no more reason why a partly shaved *Echinus* should remain permanently reared upon its equator, than that it should remain permanently inverted upon its pole; and therefore the fact that in the latter position the pedicels set about an immediate rotation of the animal, while in the former, and quite as unnatural position, they hold the animal in persistent stasis—this fact tends to show that the righting movements of the pedicels are something more than serial. Thus the whole question as between the two hypotheses amounts to whether the pedicels are able to act serially from oral to aboral pole. Observation has shown us that they are so, for we have seen *Echini* spontaneously rear themselves from their normal position on the oral pole, to the position of resting upon their equators. Further, as additional evidence that the righting movements are at least assisted by some centralising influence, is the fact that when the evolution is nearly completed by the pedicel-rows engaged in executing it, the lower pedicels in the other rows become strongly protruded and curved downwards, in anticipation of shortly coming into contact with the floor of the tank.

But, on the other hand, there is evidence to show that the action of the pedicels in executing this manœuvre, although, as we have seen, in some measure, is not exclusively dependent upon this centralising influence; and we found that the centre from which this influence proceeds is the nerve-ring that surrounds the lantern. For when this is removed, the following results are produced. The pedicels have their spontaneity impaired, though not destroyed—the animal still continuing to crawl, but only feebly, and no longer in a determinate manner, frequently changing its direction of advance, and showing a marked tendency to rotate upon its vertical axis. Moreover the echinus is now no longer able to escape from injury, but when stimulated crawls indifferently in any direction. Thus, removal of the nerve-centre seriously impairs the activity of the pedicles, and totally destroys their co-ordination. Yet when specimens so mutilated are inverted, one out of every four specimens is able to right itself. This, however, is only done with much difficulty and after a long time, so that, under these circumstances, the execution of this manœuvre seems to be just barely possible. Still the fact of its being possible at all proves that the integrity of the nerve-centre is not absolutely essential to its performance. Therefore, as experiment has failed to reveal to us any other general nerve-centre in the animal, and as even a segment of the

animal containing only a single row of pedicels is in many cases able to perform this manoeuvre, we conclude, as already stated, that the action of the pedicels is partly of a serial character, though largely assisted by the co-ordinating influence that emanates from the nerve-centre.

The effect of this operation upon the spines and pedicellariæ still remains to be considered. No effect at all is produced upon the pedicellariæ; but upon the spines a profound influence is seen to be exercised. Their spontaneity, indeed, remains unimpaired, as does also the function which they share with the pedicellariæ of closing round any instrument of stimulation; likewise their power of responsive bristling all over the animal when any part of the animal is severely stimulated continues to be manifested as before, although for an hour or two after the operation this power is suspended by shock. But the general *co-ordination* of the spines is totally and permanently destroyed, for if the animal be placed upon a table and a spirit-lamp flame held against one side, although all the spines will manifest their bristling movements (if the period of shock has been allowed to pass away), they will no longer co-operate to remove the animal from the source of irritation. These facts prove, 1st, that the general co-ordination of the spines is wholly dependent upon the nerve-centre; 2nd, that the spontaneity and local reflex irritability are wholly independent of that centre—they depend entirely upon the external nerve plexus; and, 3rd, that the universal nervous connexions revealed in the bristling movements of the spines, and which, as shown by previously narrated experiments, depend upon the hypothetical internal nerve plexus, are themselves in nervous connexion with the nerve-centre. For only thus can we explain the long period of shock which removal of this centre entails upon the functions of this supposed internal plexus. Nevertheless, the fact that these functions are eventually resumed in the general bristling of the spines, proves that this general communication between the spines is maintained by the direct conductivity of the supposed internal plexus, and is not of the nature of a reflex action, in which the nerve ring is concerned as a general centre for the responsive, as distinguished from the co-ordinated, action of the spines.

These results taken together prove that all parts of the nervous system of the Echinodermata are, in function as in structure, both central and peripheral, although the nerve-ring exercises a larger share of centralising influence than does any other part of the system.